DEPARTMENT OF SUMMARIES

TO BE DEVOTED TO DIGESTS OF PROGRESS
IN BIOLOGY

While the *Transactions* will continue to be primarily a Journal of research in micro-biology, it is recognized that the field has become so broad as to preclude the possibility of frequent articles in any one of the departments of special interest. Because of this it will be the policy to present, from time to time, supplementary digests of the progress being made in the various fields of micro-biology. It is also proposed to introduce similar summaries of the progress made in some departments not represented in our articles of research. This is done with the feeling that such reviews will increase the permanent value of the *Transactions* to all who may not have access to a large list of technical biological journals, nor the time to make the survey for themselves.

THE THEORY OF NERVE COMPONENTS AND THE
FORE BRAIN VESICLE OF VERTEBRATES

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A critical review of the two recent papers on the fore brain vesicle of vertebrates by J. B. Johnston (4) and C. J. Herrick (3) would be out of place in a short sketch. They should be consulted by those caring to follow the descriptions and arguments on which their conclusions are based. Several points in these papers have an important bearing on the theory of nerve components and a discussion of these in connection with some of the more general conclusions of that theory may not be inopportune for those whose interest in other fields of work preclude their following closely the development of the theory and its implications.

The theory of nerve components in its narrow sense, and as first worked out, applies primarily to the composition of the cerebral nerves. It has, however, extended its field until it involves not only the peripheral nerves and sense organs, but the fundamental structure of the cord and brain as well as the embryology of all these structures. It has gradually been enlarged into what has been called a functional morphology of the nervous system by applying to the

whole nervous system principles first applied to limited parts of that system.

The significance of the theory is, however, most apparent from a statement of the facts upon which it was founded.

Any one who has had occasion to consult the neurological lit- erature of the last decade preceding 1900, must have been struck by the diversity of opinion and often by the hopeless lack of agree- ment as to the homology of the cerebral nerves in the various classes of vertebrates. Coupled with this disagreement as to the homology of the cerebral nerves was disagreement as to the more fundamental problems of head morphology, particularly the problem as to the number of head neuromeres and the relation of these to the cerebral nerves and of the cerebral nerves to the spinal nerves.

Now while these fundamental problems are of the greatest in- terest and of far reaching importance to the vertebrate morphology, the question arises as to whether the point of view from which the work was done might not have had some fundamental weakness about it that prevented agreement among workers.

The dominant note, in the writer's estimation, in the neurolog- ical work of the period mentioned, was the serial homology of the central and peripheral nervous systems; not always the avowed object of research of course, but the dominant idea by which most morphological conceptions were tested.

Starting with the two-root segmental spinal nerves, the effort was made to unravel the cerebral nerves on the basis of their rela- tion to the spinal nerves; to determine the number of head segments; to place the cerebral nerves in their proper segments and to deter- mine the homology of the cerebral nerves to each other in the vari- ous groups of vertebrates. The aim was purely morphological and its weakness as a working hypothesis became most apparent in the effort to determine the homologies of the cerebral nerves with the two root theory and serial homology as the fundamental ideas back of the analysis. Much of the morphological work was extremely valuable and necessary to the solution of problems in head mor- phology which we shall have with us for a long time to come, and to which we must return from time to time and attempt to solve from a

different standpoint, and after the acquisition of new material bearing on these problems.

The essential weakness of any purely morphological conception as a working basis lies in the fact that it fails to take cognizance of the fact that an organism is primarily a living thing; that there are certain processes that it must carry on to meet the requirements imposed upon it by its environment and that no structure, however perfect anatomically, can persist and become a permanent part of the organism, if it does not do the work demanded of it. In short, what an animal has to do and the way it does it are more important and furnish a better working basis in the attempt to understand its nervous system, than the serial homology of its parts or any other purely morphological conception that ignores the function of the structures concerned. The primitive morphological characters of the nervous system may be modified almost indefinitely so long as they serve the primary functions of conduction and correlation that adjust the organism to its environment.

These criticisms of the early workers in neurology do not apply to them only, for their morphology was exactly in line with the morphology of the time. It had the same strength and the same weaknesses that the purely morphological conceptions in zoology and embryology had. The parallelism goes further. The general adoption of the experimental method in general zoology and embryology was coincident with the appearance of the theory of nerve components and a functional analysis of the central and peripheral nervous systems of the vertebrates. This I take to be the deeper significance of the recent work on the nervous system whether it is strictly experimental or not; not so much to ignore morphological conceptions as to make them of secondary importance to functional conceptions. It amounts to determining the simplest conduction paths in the lower vertebrates and following the elaboration of these paths in the more specialized higher forms, the conduction path being primarily the expression of an important functional fact.

Take for instance Gaskell's (1) treatment of the typical spinal segment. Instead of the old two-root theory which was a most serious handicap to the correct interpretation of the homologies of the cerebral nerves, he finds four roots; two somatic and two vis-

ceral, with a sensory and motor component in each. This gives us four roots to each segment and four centers in the cord. The terms used to designate these components, somatic and visceral, are of course morphological as are their homologues in the brain; but the significance really lies in the fact that the visceral sensory and visceral motor components are concerned in reflexes involving the adjustment of internal organs to each other, while the somatic motor and somatic sensory components are concerned in reflexes involving the adjustment of the organism to its external environment through external stimuli and by means of somatic muscles concerned chiefly in locomotion.

By conceiving of these four centers of each segment as arranged in longitudinal columns, we can speak of a longitudinal analysis of the cord, even though the centers may not be continuous as cell masses in consecutive segments. This conception of longitudinal columns of the cord and brain, while it does not clear up some of the difficulties encountered by the students of transverse seg- mentation of the brain, furnishes us with a far more valuable con- ception with which to attack the fundamental problems of the cord and brain. It shows how simple generalized reflexes have been elaborated into highly specialized reflexes, particularly those of the special senses and of the higher types of conduction paths of the higher mammals.

This idea was first clearly enunciated for the brain by Johnston (5) on the basis of his study of the brain of the sturgeon. Here we find an almost diagrammatic arrangement of the four columns with a marked continuity throughout the length of the medulla. The simplicity of arrangement is due in part to the hypertrophy of the columns and in part to the widening of the central canal of the cord into the fourth ventricle. From the medulla the columns extend forward into the regions anterior to this with varying degrees of continuity; the important segmental nuclei of the metencephalon, the mesencephalon and the diencephalon being referable to these four columns. The conduction paths are important in determining the exact relation of important regions in the segmental portions of these three brain divisions and the supra-segmental centers are refer- able to correlation tissue present to a greater or less extent in segmental centers.

The older morphology sought to place these centers in their proper places in the transverse segmentation of the brain, an effort that met with indifferent success and when successful gave us little clue to the functional significance of the centers. The newer morphology inquires primarily as to which of the four functional divisions, as shown most distinctly in the medulla, a particular nucleus or tract belongs, and concerns itself only secondarily with its place in the transverse segmentations of the head, since its relation to one of the four functional divisions determines its position functionally and serves to explain the significance of the secondary and tertiary reflex paths in the brain.

Turning now to the cerebral nerves, to which the theory of nerve components was first applied in its narrow sense, we find that the first analysis of the cerebral nerves on the basis of their components or functional units was made by Strong (6) on an amphibian. This analysis was very thorough for the trigemino-facial complex. Somewhat later a very thorough analysis of all the cerebral nerves in a teleost was made by Herrick (2) accompanied by a full description of the central connection and peripheral distribution of these nerves. The basis upon which this analysis was made is the difference in size between the fibres of the various components such as the ear and lateral line or acoustico-lateralis component, the general cutaneous or tactile, and the visceral including both special visceral or gustatory and the general visceral supplying mucous surfaces. The analysis is simplified in some types by a complete isolation of ganglia which are usually fused in other types and especially by the hypertrophy of certain of these systems—in some types one, and in other types another—so that the course of a given component can be traced from its origin in its ganglion to both its central and peripheral terminations. This last principle of using hypertrophied systems has been emphasized and used, particularly by Herrick, in the solution of difficult problems in the morphology of the brain and nerves. It practically amounts to selecting a type in which nature has performed an experiment for us, as for instance in the case of the enormously hypertrophied gustatory system of the catfishes where this system is so large in proportion to other systems that both its peripheral nerves and central connections can be fol-

lowed with comparative certainty. A great deal of attention has been paid in nerve component work to the analysis of V, VII, VIII, IX and X nerves, particularly their sensory components because these, excepting the VIII, are compound nerves. The III, IV and VI are pure motor nerves and easily referable to the somatic motor group and I and II stand, in a sense, in a class by themselves owing to their mode of development. These nerves are amenable to the same classification, the I being placed in the visceral sensory and the II in the somatic sensory division. These will be referred to later.

Without attempting to give in any detail the distribution of the three components mentioned, the general cutaneous, the acoustic-lateralis and the visceral in the cerebral nerves, the general statement may be made, taking the ganglia as a starting point, that in the Ichthyopsida the V ganglion furnishes only general cutaneous or tactile fibres. The VII ganglion furnishes, from two of its divisions, lateral line fibres and from a third division visceral fibres both special gustatory and general. The VIII ganglion furnishes only auditory fibres referable phylogenetically to the lateral line group. The IX ganglion contains in *Ameiurus* apparently a pure special visceral portion whose fibres supply taste buds and a lateralis ganglion. The X contains all four components.

The way in which these components are distributed in any given cranial nerve trunk is quite variable. A particular nerve in two different types retains its integrity only in a general way, the degree of variability depending largely upon the dominance of one or the other of these components. So that nerves vary not only in the relative amount of any one of these components and consequently in their mode of peripheral distribution but vary absolutely also by containing components in one type which are absent in another. The peripheral organs to which any one of these components is distributed are constant, as are their central connections in the brain, and these central connections are referable to the four longitudinal columns mentioned earlier.

The most obvious conclusion from a study of the analysis of the cerebral nerves is that the units of which the cerebral nerves are made up are the components and not the nerves themselves. Any given cerebral nerve if studied in a number of types is likely to

show a variation in its distribution owing to the fact that it does not have a constant structure. The cerebral nerves are more like routes from the periphery to the brain in which the units of conduction vary. The components consequently become the units in our analysis of these cerebral nerves and the term nerve-component becomes extremely valuable as a constant reminder that we must start with these as a basis in our attempt to analyze the cerebral nerves rather than the segmental position of the nerve, with reference to head neuromeres. The determination of the precise segmental position of a given cerebral nerve would be an interesting morphological fact if we could ascertain it exactly, but is relatively unimportant compared with an accurate knowledge of the functional divisions or components of the nerve which enable us to determine what kind of reflexes must be served by this nerve, and the part it plays in the economy of the body as a functioning organism. The theory of nerve components looks toward an explanation of how the nervous system works.

The interesting question of the relation of the head to the trunk is not ignored in the theory of nerve components, although it is approached from a different point of view. The terms "general cutaneous" and "general visceral" applied to fibres in the cerebral nerves that do not end in special sense organs, indicate the fundamental similarity of these in both brain and cord. This conclusion is further strengthened by the similarity in mode of origin of the two components in the brain and cord, these coming from the neural crest in both cases.

The relation of the special somatic components of the cerebral nerves, in which class the acoustico-lateralis and optic fibres fall and of the special visceral, in which class the gustatory and olfactory fibres fall, is not quite so simple. These classes of fibres receive their name from the fact that they end in the cord and brain in centers homologous to the visceral and somatic centers of the cord and are special in the sense that they end in specialized organs. They differ from spinal nerves in the fact that there are in present Ichthyopsida no homologues of the special sense organs in the trunk innervated by spinal nerves and that the specialized ganglia arise in a manner totally different from the spinal ganglia. The

fact that the centers in the brain are homologous to those of the cord enables them to be placed in the same general category from a functional standpoint.

Whatever may prove to be the explanation of the origin of the special sense organs and of the special ganglia, the reference of the special components of the cerebral nerves to the two components represented in the cord is a marked step in the direction of a rational interpretation of the marked cephalization of the vertebrates.

Returning now to the brain axis, we find the attempt made in the two papers mentioned to carry the analysis of the brain stem into the diencephalon and telencephalon. Prof. Johnston has given his attention mainly to the question as to the exact delimitation of the first two segments, while Prof. Herrick has taken up the question of the extension of the four longitudinal columns into the first two brain segments.

Both these papers contain suggestions for changes in the B. N. A. subdivisions of the diencephalon and telencephalon. The bearing of the papers on the analysis of the brain axis into logitudinal columns, only, can be taken up here.

In the diencephalon the six primary laminae of His, i. e., the roof plate, the floor plate and two lateral plates on each side become ten according to Herrick. The two lateral plates of His which are separated by the longitudinal furrow, the sulcus limitans, are divided into four longitudinal regions by two additional furrows. The two dorsal columns of these four lateral columns are devoted mainly to receptive functions and the two ventral columns to effector functions. The ventral columns contain chiefly the descending conduction paths and the dorsal the ascending conduction paths. The sulcus limitans disappears in the diencephalon and its disappearance is probably correlated with the absence of motor nerves anterior to the mid-brain and to the invasion of the remaining motor coordination tissues by visceral elements. The evagination of the optic vesicle occurs in the dorsal lamina. The boundary between the diencephalon and telencephalon is placed by Johnston on a line running from the velum transversum to the chiasma. This leaves a median unpaired portion in the telencephalon in addition to the

paired portions evaginated from the brain axis and surrounding the first and second ventricles.

Prof. Herrick's analysis of the telencephalon is based upon the adult amphibian and the embryonic brains of vertebrates generally.

The four lateral columns of the diencephalon are evaginated to form the hemisphere but owing to the meeting of the roof and floor plate of His in the lamina terminalis or rostral end of the brain, the columns situated at the extreme dorsal and the extreme ventral parts of the lateral brain wall approach each other and are shifted in position so as to meet on the medial wall of the lateral ventricle leaving the lateral wall to be formed by the two middle columns of the diencephalon.

The two ventral laminae are directly continuous with the ventral columns and are concerned in efferent functions, the ventromedial in visceral efferent and the lateral in somatic efferent functions.

The two dorsal laminae correspond to the two dorsal laminae of the diencephalon but direct continuity between the two regions of the brain is interrupted in forms above fishes by the great flexure between the diencephalon and telencephalon. The olfactory bulb was the site of the initial telencephalic evagination, but later in phylogeny all four columns become involved and there was also much differentiation *in situ*. The later stages of the telencephalon were dominated by the entrance of tracts for the correlation of olfactory sense with tactile and visual sensations and as we ascend the phylogenetic series the non-olfactory correlation tissue dominates more and more the functions of the telencephalon.

The significant fact about both these papers is not so much the explanation of later stages of the first brain vesicles, although that is significant, as the reduction of them to a simple type which brings them into line with other parts of the brain axis and renders clear the analysis of the whole brain axis from a functional standpoint. It is a significant step in the process of rendering intelligible the most puzzling field in vertebrate anatomy.

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